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TRANSACTIONS
of
THE NEW YORK ACADEMY OF SCIENCES

SER. II, VOL. 7 APRIL, 1945 No. 6

SECTION OF GEOLOGY AND MINERALOGY

MARCH 5, 1945

DOCTOR WALLACE M. CADY, Geologist, Alaskan Branch, United States Geological Survey, Washington, D. C.: *Aerial Photographs as an Adjunct to Arctic and Sub-Arctic Geologic Reconnaissance.** (This lecture was illustrated with lantern slides.)

The usefulness of aerial photography in the mapping of desert regions where bedrock is well exposed has been rather obvious for a long time. Geologic structures and more highly colored formations exposed in desert ranges are commonly registered in detail on aerial photographs and may be plotted directly on maps made from the photos, reducing the ground survey from a long, tedious, routine, mechanical procedure to a reconnaissance of critical localities guided by the photographs. In sub-arctic and arctic regions, aerial photos are particularly useful because, due to a heavy cover of tundra moss and frost-heaved ground, particularly in unglaciated regions, such as in the greater part of interior Alaska, geologic structures hard to recognize at close hand on the ground become visible from the air. In recent years, the U. S. Army Air Forces have photographed much of arctic and sub-arctic North America from the air, revealing geologic features previously unrecognized, although ground surveys may have already been made. Certain of the photographs released to the Geological Survey for official use have become a valuable adjunct to geologic reconnaissance in Alaska, undertaken primarily as an inventory of Alaskan mineral resources.

* Published by permission of the Director, U. S. Geological Survey.

TRANSACTIONS of the New York Academy of Sciences, Series II, Volume 7, No. 6, April, 1945.
This publication is distributed to Members and is published monthly from November to June, inclusive, at 109 West Chestnut Street, Lancaster, Pa., by The New York Academy of Sciences, Seventy-ninth Street and Central Park West, New York City.
Editor: Roy Waldo Miner.
Executive Secretary: Eunice Thomas Miner.
Entered as second-class matter December 2, 1938, at the post office at Lancaster, Pa., under the act of August 24, 1912.

Up to the time the aerial photographic surveys were begun, large areas amounting to at least half of Alaska remained unexplored. The photographic compilation has shown the distribution of drainage features in these hitherto unexplored areas, but ground surveys are still necessary to establish topographic and geologic control.

One of the larger unexplored areas in which the aerial photographs are being used in connection with ground surveys is the central Kuskokwim region, west of the Alaska Range and south of the Yukon River. Here the Kuskokwim River, second largest in the Territory, cuts westward in a relatively narrow gorge through the Kuskokwim Mountains and flows southwestward into the Bering Sea. The scattered higher peaks of the Kuskokwim Mountains, reaching altitudes averaging about 3,500 feet, have been maturely glaciated, but by far the greater part of the region is maturely dissected by streams forming well-rounded hills averaging about 2,000 feet in altitude with 500 to 1,000 feet of relief. The rounding and smoothing of the slopes have been accentuated by frost weathering. The climate is sub-arctic, i.e., the region lies south of the sea-level isotherm of 50° F. for the warmest month of the year. However, the hills and mountains above 1,000 feet altitude are bare of trees and the upland weather is comparable with that of the typical arctic tundra north of the warm-month isotherm of 50° F. and the poleward limit of forests. Spruce is the principal forest tree that covers the bottomlands. The light gray-green lichen, known as caribou or reindeer moss, covers the broad upland slopes.

The relatively wide expanses of upland tundra, cut by such deep narrow valleys as that of the Kuskokwim River, promote the optimum usefulness of aerial photographs as an adjunct to geologic reconnaissance. The bedrock features are best exposed in the cut-banks and bluffs along the main streams where frost action has not kept pace with stream cutting as it has on the uplands back from the streams. Here, small geologic structures of no greater magnitude than the length and height of the exposure may be made out, but, except possibly along the rather continuous gorge of the Kuskokwim River, the exposures are separated from one another by broad expanses of tundra, across which it is commonly difficult to connect the smaller structures through ground surveys alone.

The predominant bedrock formation of the region is a very thick succession of interbedded graywacke and shale of Upper Cretaceous age bordered on the northwest and southeast by Paleozoic formations.

Ann. New York Acad. of Sciences
7-2-45

The graywacke strata form faint ridges that are either entirely imperceptible on the ground or, as slope traces, are difficult to orient. These faint ridges and traces are readily distinguishable on aerial photographs taken at 20,000 feet. A variety of Tertiary igneous rocks, ranging from basalts to granites, is found in the region, although it is not as extensive as the graywacke and shale. Granitic rocks form stocks and cupolas with roughly circular groundplans; intermediate types form elliptical stocks and sills, conforming in orientation to structures in the graywacke-shale succession; and the basaltic rocks form thick surface flows or small tabular intrusives, principally sills. These igneous features are readily identified on the ground as they are rarely weathered down to the point where they are completely covered by tundra moss or foreign solifluction products. However, the granitic to intermediate intrusives, in particular, are recognizable on the aerial photographs because of their size and shape. Contact metamorphic zones are found in the graywackes and shales bordering the granitic stocks. The outer limits of these zones are about at the edge of the maturely glaciated areas among the higher peaks and thus are recognizable on the aerial photos. Talus slopes are developed much more extensively on the metamorphic rocks than on the granite forming the cores of the peaks, making it possible to tell the two apart.

Regional geologic structures are shown in more detail by the pattern of surface traces revealed on the aerial photographs than would be possible in standard ground-reconnaissance practice. Plotted photogrammetrically the traces form the basis of useful tectonic maps in areas where slope cover inhibits ground surveys. Thus far, ground surveys, particularly along river courses, have revealed rather tight minor folds in the Upper Cretaceous graywackes and shales. Major folds of greater extent than the individual exposures have been difficult to identify, due to the lack of good key strata that would assist structural interpretation in connection with either ground or aerial surveys. However, the trace pattern of areas between ground surveys, completed to date, suggests rather convincingly the orientation of fold axes, in general northeasterly, but with a tendency to parallel the contact of bordering Paleozoic formations, regardless of the orientation of the latter. Major high angle faults which have been passed over unnoticed on the ground are distinguishable on the photographs. The faults are particularly well developed along the borders of the Kuskokwim Mountains. Their nearly unbroken traces cross the bedding traces indicating that

the faults are later than the folds and probably related to a differential uplift of the Kuskokwim Mountains, following folding.

Of the various ore minerals prospected for and mined in the central Kuskokwim region, gold lies closest to granitic and intermediate igneous intrusives, such as are recognizable in the aerial photographs. Although lode gold has not been mined here, several groups of placer claims have been staked and operated in the vicinity of large rhyolitic sill-like bodies, certain of which are in close proximity to one of the granitic stocks. Tin and tungsten minerals are found in some of the placer concentrates with the gold. Quicksilver, the principal mineral product of the region, is found chiefly in or close to altered basic intrusives which have weathered deeply and are not in themselves large enough to be detected on the aerial photographs. The ore mineral, cinnabar, accompanied by varying amounts of stibnite, has been found in veins cutting the altered basic rocks and, to a lesser extent, in the other types of intrusives, except stocks of typical granites. The latter do not crop out in the areas in which cinnabar is found. Quicksilver metalization may be related to more deep-seated intrusives than those in their vicinity at the present surface, possibly parts of the granite, not yet unroofed, or deeper zones of the other intrusives. It is hoped that further study of the regional geology will help clear up this problem and thereby suggest guides in locating new quicksilver lodes in yet unexplored areas.

It is anticipated that, as an outcome of widespread aerial photographic surveys made in recent years, photogrammetric analysis of geologic features will soon become a very important preliminary to ground reconnaissance of unexplored regions in the search for new mineral reserves. As already stated, analyses of data obtained from aerial photographs of arctic and sub-arctic regions, such as those of Alaska, which, incidentally, constitute the greater portion of unexplored country, are particularly useful, because many geologic features seen in the photographs cannot be seen on the ground. It is hoped that simple, refined techniques and instruments will be developed to reduce surface trace lineations, however minute, to lines of known orientation from which the geologist can plot the dip and strike of planar structural elements for use in both tectonic maps and structure sections. Such analyses would be substantiated by ground examination of critical areas analogous to the ground control necessary for topographic mapping from aerial photographs.

SECTION OF BIOLOGY

MARCH 12, 1945

DR. ALEXANDER SANDOW, Assistant Professor of Biology, Washington Square College of Arts and Science, New York University, New York, N. Y.: *The Mechanism of Energizing Muscular Contraction.* (This lecture was illustrated by lantern slides.)

It is now generally agreed that the two most fundamental components of muscle are the fibrous protein, myosin, and the nucleotide, adenosinetriphosphate (ATP). Myosin, the principal component of the myofibrillae, is the contractile substance, while ATP, abundantly supplied with chemical potential energy in its two labile phosphate bonds, is the substance that directly energizes myosin for its mechanical activity. The basic problem of muscular contraction is to determine the mechanism by which the stored energy of ATP is transferred to myosin and converted by it into mechanical energy. In the discussion to be presented here, we shall limit ourselves to only the first phase of this problem, i.e., to the nature of the process by which the energy of the labile phosphate bonds of ATP is transferred to myosin.

A uniquely significant contribution to the solution of this problem is found in the discoveries of Engelhardt and his coworkers (1939, 1941, 1942) that (1) myosin acts as adenosinetriphosphatase, i.e., it is an enzyme, specifically catalyzing the hydrolysis of ATP to adenosinediphosphate (ADP) and free inorganic phosphate with the release of the 11,000 cal/mol PO_4 of the last phosphate bond of ATP; (2) artificially spun myosin fibers undergo an elongation in the act of splitting ATP. These findings are important, for they offer additional proof, if this be needed, that ATP is the direct energy source for myosin; and they suggest, furthermore, that the process by which the energy transfer is affected is a function of the enzymatic activity of the contractile substance and that this transfer is associated with the relaxation of myosin in some phase of the mechanical response of muscle.

One approach to the energizing problem is concerned with the temporal aspects of the interaction of myosin and ATP in relation to the sequence of latent, contraction, and relaxation periods that normally occur in a muscle twitch. Two general *a priori* possibilities exist. In the first, which we designate *activation coupling* (Ritchie's (1933) "Chemical" Theory), the transfer of energy to myosin occurs simultane-

ously with the direct activation of the contractile process in the latent and contraction periods; in the second, *recovery coupling* (Ritchie's "Physical" Theory), the energy transfer is affected during the relaxation period, and, more generally, probably also during some of the immediate post-relaxation period. In activation coupling, the stimulus applied to a muscle serves to initiate the interaction of myosin and ATP and this not only energizes myosin, but also activates it to develop tension. Thus, ATP would be not only the energizer of the contractile substance, but also the agent that directly stimulates it to contract. Recovery coupling, on the other hand, would involve the basic myosin—ATP reaction in the general post-contractile phase of a contraction, and it would serve essentially to transform the energy released by ATP hydrolysis into some form of "physical" potential energy of the myosin molecule. Subsequent stimulation would then act to bring about a discharge of the stored energy and this would lead to tension development. In the following discussion, several salient lines of research of various workers pertinent to the above will be analyzed. Some attention will then be given to certain of our own investigations.

The work of Ritchie (1933) was the first in recent years to pose the temporal problem in energization and to suggest a choice between the two possibilities. In conformance with the generally held view in the early 1930's, Ritchie assumed that creatinephosphate (CP) was the direct energy source for the contractile material. Since the rate of breakdown of this substance is decreased by increase in pH, he varied the pH of a muscle (the frog ventricle) and measured the corresponding changes in rate of activation and recovery processes in the response of this muscle. He found that the rate of activation, as measured by the duration of the latent period, was negatively correlated with the rate of CP hydrolysis. He, therefore, asserted that CP breakdown was connected with some recovery reaction, and thus concluded in favor of recovery coupling. (Ritchie's research also included experiments on the refractory period, but since this period is essentially connected with the excitatory aspect of muscle behavior, the results do not seem to be relevant to the present discussion, which is concerned with the contractile system. Incidentally, however, it is of interest to note that the variation in duration of the refractory period indicated that the speed of the recovery process implicit in this part of the excitatory reaction was found to be positively correlated with the rate of CP hydrolysis.)

Although Ritchie's experimental results are correct, their interpre-

tation today is faulty, since we know that ATP, and not CP, is involved in the direct energetic coupling of myosin. Now, in the physiological range of pH, varying the hydrogen ion concentration affects the rate of hydrolysis of ATP oppositely to that of CP. Thus, the rate of tension onset, as measured by the length of the latent period, is positively correlated with the speed of ATP hydrolysis. Hence, properly interpreted, Ritchie's results favor activation coupling.

Further evidence for activation coupling may be found in the important finding of Brown (1936) that extra tension in the isometric twitch of the turtle retractor penis muscle and the frog sartorius is induced by suddenly applied high pressure (272 atmospheres) only during the initial eighth of the contraction period. This result suggests that the highly pressure-sensitive process is a chemical reaction which is concerned with the mobilization of energy for contraction, and since this reaction occurs early in the contraction period, activation coupling would be involved.

Another source of evidence for activation coupling is found in the experiments of Buchthal and his co-workers (1944, a and b) which have demonstrated that, when ATP is directly applied to frog skeletal muscles or their isolated fibers and to mammalian smooth muscles, a contraction is initiated which involves, in all cases, a fall in birefringence of the activated muscle structures. Since "these experiments support the view that ATP is an essential agent in the release of normal muscular *contraction*" (my italics, A.S.), they lead to the conclusion that the energetic coupling of myosin and ATP occurs in the activation period.

Finally, as favoring activation coupling, there will be discussed the work of Dr. Joseph Needham and his coworkers (Dainty *et al.*, 1944). This research has demonstrated, among other things, that when a myosin solution is treated with ATP, decreases immediately occur in the flow birefringence and the relative viscosity of the myosin. These changes are relatively more slowly spontaneously reversed and, during this reversal, the hydrolysis of the ATP takes place. The initial physicochemical changes in the myosin indicate that the micellae of this protein shorten, in some manner, along the direction of their long axes. Thus, contact with ATP causes the myosin micellae to contract. It is noteworthy, however, that the actual splitting of the ATP is temporally associated with the disappearance of the shortened state. Therefore, it seems that the physical basis for contraction of the micellae may be the

formation of an enzyme-substrate combination between myosin and ATP.

Dainty *et al*, state, however, that further experiments "are still needed to decide between the two possibilities: (a) That the combination between myosin and ATP so alters the myosin molecule, that reaction between some groups along the length of the chain becomes possible and provides energy. The subsequent splitting off of phosphate from the substrate would then supply energy needed for relaxation and recharging of the myosin fibril. (b) That the splitting off of phosphate and setting free of energy from the ATP accompanies the contraction." It thus appears that the results of the Needham group cannot be unequivocally interpreted in all their aspects. But, nevertheless, it is, clear that ATP acts as an agent that causes myosin micellae to contract and, hence, in so far as the results of model experiments may be applied to the analysis of the contraction of live muscle, this finding points to a type of activation coupling mechanism.

Evidence will now be presented that seems to favor the recovery coupling mechanism. Kalckar (1941) calls attention to the very suggestive fact that, after sufficient activation of iodoacetate-poisoned muscles, there results, terminally, a mechanical condition of fatigue and rigor with which is associated a chemical state of extreme irreversible depletion of the ATP and CP stores. It is inferred that the inability to relax and contract, as indicated, respectively, by the rigor and the fatigue are the consequence of the absence of ATP and CP. Therefore, it is hypothesized that, in the normal muscle, which is rich in ATP and CP, relaxation occurs as a result of a coupling of these substances to myosin and that, during this process, the myosin is energized for a subsequent contraction. We may disregard the inclusion of CP in this process, since it can be only indirectly concerned with the energization of myosin by virtue of its role in the resynthesis of ATP. The mechanism proposed by Kalckar, however, is a form of recovery coupling. In criticism of this hypothesis, it may be mentioned that the rigor of iodoacetate fatigued muscles could be the result of metabolic disturbances, other than the depletion of ATP or CP, that are characteristic of the action of this drug. Furthermore, rigor does not necessarily accompany inability to contract, as is seen, for example, in completely fatigued normal muscles.

Engelhardt's finding (1941, 1942) that enzymatically active myosin threads suffer a relaxation has been used by him as a basis for the view

that the post-contractile relaxation of a contraction is the phase of a muscular response, during which myosin catalyzes the breakdown of its substrate, ATP. Thus, according to this view, the energizing of myosin for contraction is a function of the relaxation period. But Engelhardt was evidently unaware of the existence of a pre-contractile relaxation, the latency relaxation (LR) (Rauh, 1922; Sandow, 1944), which will be fully described later. If muscular relaxation is an *in vivo* sign of the coupling of myosin and ATP, then this interaction may be going on at the time of the LR. Hence, although Engelhardt interprets his experimental results so as to suggest a form of recovery coupling, an alternative interpretation which takes into account the LR, a latent period event, suggests that the energizing mechanism involves activation coupling.

It is evident that the investigations discussed thus far do not permit us to draw an indubitable conclusion concerning the mechanism of muscular energetic coupling. In so far as interpretations are based on experiments with purified extracts of myosin and ATP, we note that the Engelhardt view favors recovery coupling, while that of Needham group, in its most certain aspect, suggests a form of activation coupling. The contradiction between these two conceptions becomes more striking when it is realized that a basic experimental difference is involved, namely, that, despite the presence of a common specific myosin—adenosinetriphosphatase activity, Engelhardt's myosin fibers merely relax, while Needham's myosin micellae in solution first contract and then relax. The research with whole muscle presents a more unified picture. Reasons have been already given for questioning the validity of Kalckar's hypothesis. To these may be added the fact that his view is based on an abnormal—indeed, moribund—condition of muscles in iodoacetate rigor. We are thus left with the results of Ritchie, Brown, and Buchthal which favor activation coupling. Since these results were all obtained with quite normal live muscles, it would seem that this evidence is strongly weighted in favor of the activation coupling mechanism.

We shall now turn to our own investigations[1] which are concerned with studies of the latent period of frog skeletal muscle contraction, with particular reference to the latency relaxation (LR) first discovered by Rauh in 1922. A detailed description of the piezoelectric, cathode-ray oscillographic method of our experiments, and a general analysis of the

[1] Aided in part by a grant from the Penrose Fund of the American Philosophical Society.

LR will be found in Sandow (1944). An outline of these aspects of our research is given in Sandow (1945a). It will suffice here to state that the typical latent period at room temperature of a frog sartorius muscle, initially under a tension of 3 gms., begins, after the instant of application of the stimulus, with a mechanically quiescent phase having a duration, L_R, of about 1.0–1.5 ms. This is followed by a sigmoid relaxation phase, the LR, which, after achieving a magnitude, R, is abruptly reversed as the muscle, terminating the latent period, passes into its contraction period. The duration of the latent period, i.e., the time interval from the instant of stimulation to the first appearance of positive tension change, L_R, is about 3.0 ms. R is a negative tension change, generally of the order of one-thousandth of the positive tension output at peak of a twitch, and thus represents a tension decrease of about 20 mg. The precision of measurement of these events is generally of the order of $\pm$ 0.02 ms. for the time intervals and $\pm$ 0.1 mg. for the LR tension change.

The results[2] that will be discussed are concerned with the effects of pH and of temperature on the latency phenomena. The effect of pH changes, indirectly induced in the muscle by its own previous activity, is discussed in Sandow (1945, a and b). The general conclusion of this work, that the higher the pH, the shorter is L_T, has been confirmed by experiments (Sandow, 1943) in which the hydrogen-ion concentration of the muscle was directly modified over the range from pH 6.0 to 8.5 by exposing it to different mixtures of CO_2 and O_2 (or N_2) in bicarbonate-buffered Ringer's solution. Thus, we verify for skeletal muscle what Ritchie (1933) found for heart muscle. Since the tension latency, L_T, is shorter the higher the muscle pH, it is evident that the speed of some process directly determining the speed of tension onset is increased, the more alkaline the muscle. In view of the fact that the hydrolysis of ATP by myosin increases with pH (up to about pH 9.0) (Bailey, 1942; DuBois and Potter, 1943), we feel that this is the reaction occurring in the latent period that directly energizes and activates the rise of tension.

If the ATP hydrolysis that is supposed to take place in the latent period is specifically catalyzed by myosin, then it is important to search for independent proof of the involvement of the contractile enzyme. Evidence that myosin—in the sense of a fibrous protein—is involved in the formation of the LR is presented in Sandow (1944). But the in-

[2] These results were obtained in experiments performed in collaboration with Mr. A. G. Karczmar.

fluence of temperature, especially on R—the magnitude of the LR—indicates that the LR is a mechanical sign of the enzymatic activity of myosin.[3]

As the temperature is varied from 10° to 40° C., R increases to a maximum at about 24° and then falls at higher temperatures until, at 40°, it is only a few percent of the maximal value. If the muscle is kept for a minute or so at 40° and then quickly returned to the optimal temperature, 24°, the magnitude of R is greater than it was at 40°, but not as great as it was at 24°, before submission to the higher temperature. Thus, the inactivation of R at high temperature can be partially reversed. The detailed study of inactivation of R by high temperatures leads to the following conclusions: (1) The irreversible inactivation of R begins quite sharply at a critical temperature of about 37.5° and the rate of irreversible inactivation increases very rapidly within the range of the next few degrees. The temperature coefficient of this process at about 38°–39° expressed as a Q_{10} value is of the order of several thousand. (2) Another critical temperature exists at about 41°, for, at or above this temperature, completely irreversible inactivation of R occurs very quickly, i.e., in a few minutes.

The general variations of R with temperature are very similar to those characteristic of temperature effects on enzyme behavior. Therefore, it is inferred that the LR is an expression of the action of an enzyme. Furthermore, the two critical temperatures for the inactivation of R, one at 37.5°, the other at about 41°, are, respectively, essentially the same as those at which Mirsky (1937) has demonstrated the occurrence of primary and secondary heat denaturation of extracted frog myosin, and the high Q_{10} for the LR inactivation at 38–39° C. is comparable to that of the order of one thousand found at a similar temperature range for the primary denaturation process. The thermal features of the inactivation of the LR and the denaturation of myosin are so similar that we therefore conclude the LR is determined by some action of myosin. Since these generalizations concerning the significance of the temperature variations in R indicate that, on the one hand, the LR represents an enzyme action, and, on the other, a property of myosin, it is reasonable to infer that the LR is an indication of myosin acting enzymatically. This view is strengthened by the inference, derived by analysis of the effect of pH, that the hydrolysis of ATP—

[3] See Sandow (1943) for a preliminary announcement of the general effects of temperature on the latency phenomena. Only the behavior of R will be discussed here.

the substrate of myosin—is occurring during the latent period which includes the time interval of the LR.

The synthesis of the results of our pH and temperature experiments thus indicates—inferentially, it is true—that the latent period is a time interval during which myosin acts enzymatically on ATP. Indeed, if Engelhardt had not discovered the ATP-ase activity of myosin, our experiments might have been used to suggest this as a possibility. But, in view of Engelhardt's finding, the unique contribution of our research lies in the suggestion that, in the live muscle, the enzymatic interaction of myosin and ATP, and hence the energizing of myosin, take place during the latent period of the mechanical response. Thus, our work lends support to the view that muscular contraction is energized by the mechanism of activation coupling.

The question that now arises is the detailed nature of the coupling of ATP and myosin, and its relation to the sequence of mechanical changes in a stimulated muscle, first relaxation—the LR—and then, contraction. The following theory (preliminary notice in Sandow, 1943) is proposed in explanation of these events. Assume that the reaction between myosin and ATP in stimulated muscle involves the formation of an intermediate enzyme-substrate combination in accordance with the following scheme:

$$M + ATP \longrightarrow M\text{-}ATP \longrightarrow M_C + ADP + H_3PO_4 \qquad \text{(I)}$$

in which M represents myosin at rest, M-ATP, the intermediate combination, M_C, contracting myosin, and ADP, adenosinediphosphate. This scheme pictures the transfer of energy from ATP to M as a function of the intermediary, M-ATP; and when this transfer is accomplished, there are released from the intermediary, not only the energy-degraded products of the hydrolysis of ATP, but also the energy-enriched and contracting myosin, M_C. Since M corresponds to the muscle at rest and M_C to contracting muscle, it is therefore supposed that the intermediate M-ATP is the form of myosin responsible for the LR that intervenes between rest and contraction. In other words, we specifically assume that the LR is a mechanical sign in live, stimulated muscle of the presence of the enzyme-substrate combination, M-ATP.

In addition to evidence already adduced in support of our assumption concerning the significance of the LR, we may point to the result of Engelhardt that myosin threads elongate in association with their enzymatic activity. It is possible that this elongation corresponds to

the formation of an M-ATP complex. It is true, in the Engelhardt experiment, that, even though the ATP was hydrolyzed, the myosin threads remained extended; but the failure to contract may be a consequence of the processes of extraction and formation of the myosin into threads. Be that as it may, our assumption is in direct contradiction to the view of the Needham group that *contracting* myosin is represented by the M-ATP combination. But this view is an inference. Furthermore, it is based on experiments with myosin in solution and not in the form of fibers; and, as Dainty *et al.* (1944) state, "It must be remembered that, *in vitro*, the contraction of the myosin particles does no work, and the conditions are therefore very different from those *in vivo*." Therefore, it does not seem to be too arbitrary to adopt the contrary assumption concerning the role of M-ATP that we have included in our theory. Finally, the possibility should be mentioned that the behavior of myosin in live muscle may represent a synthesis of the mechanical behavior of extracted myosin found in the Engelhardt and Needham experiments; i.e., the LR corresponds to the elongation of Engelhardt's myosin fibers, and the subsequent contraction and relaxation are equivalent to the shortening and then lengthening of the Needham micellae.

Since, in our theory, M-ATP is the LR form of myosin, we will designate it by M_R. If it be now assumed that the reactions, $M \rightarrow M_R$, and $M_R \rightarrow M_C$ are, in first approximation, monomolecular, with velocity constants k_1 and k_2, respectively, then the determination of the course of the mechanical change of the stimulated muscle reduces, in the first place, to the problem of the kinetics of the following chain of reactions:[4]

$$M \xrightarrow{k_1} M_R \xrightarrow{k_2} M_C. \qquad \text{(II)}$$

M_R and M_C will not exist in the unstimulated muscle. Hence, taking the initial concentration of M equal to unity, we have, as the initial conditions for Reaction (II) (using small m's to represent concentrations): $m = 1$, $m_R = m_C = 0$. The solution of this system giving the m's as a function of time, t, is well known:

[4] A formally identical reaction system, but with different meanings attributed to the reactants, has been proposed by Gilson, Walker, and Schoepfle (1944) as a theoretical basis for the course of the tension output in a muscular contraction. The relation between this theory and ours will be discussed elsewhere.

$$m = e^{-k_1 t}, \tag{1}$$

$$m_R = \frac{k_1}{k_2 - k_1}\,(e^{-k_1 t} - e^{-k_2 t}), \tag{2}$$

$$m_C = 1 - \frac{k_2}{k_2 - k_1}\,e^{-k_1 t} + \frac{k_1}{k_2 - k_1}\,e^{-k_2 t}. \tag{3}$$

Thus, the tension development of the muscle; i.e., the change from the resting state of M, will be given by some function of the quantities m_R and m_C. Now, for large values of the time, $m_R \to 0$, and $m_C \to 1$. Thus, for $t = \infty$, all the myosin is in the contracted state, and this, it is assumed, will correspond to the time of maximum tension in a tetanus. For simplicity, set this maximum tension equal to unity.

At present, there is no basis for choosing a particular form of the function of m_R and m_C to represent the tension development. With a first approximation in mind, however, we will make the assumption that the tension, T, of the muscle, at any instant, is given numerically by the difference between m_C, the concentration of the contracted myosin, and m_R, that of the relaxed intermediary myosin. Hence,

$$T = m_C - m_R \tag{4}$$

and, using the expressions given in Equations (2) and (3),

$$T = 1 - \frac{k_2 + k_1}{k_2 - k_1}\,e^{-k_1 t} + \frac{2k_1}{k_2 - k_1}\,e^{-k_2 t}. \tag{5}$$

Omitting the analytical details here, a first study of Equation (5), in comparison with experimental curves for the time-course of the usually recorded isometric tension production in a tetanus, and for the latency relaxation of a frog sartorius muscle at about 20° C., leads to the choice of the values: $k_1 = 20$, and $k_2 = 800$. Inserting these values in Equation (5), we have,

$$T = 1 - 1.0513\,e^{-20t} + 0.0513\,e^{-800t} \tag{6}$$

A plot of this equation shows that the tension curve is strikingly similar to corresponding experimental myograms of a tetanus. But of greatest interest is the fact that Equation (6) includes an initial phase involving a very slight and short negative tension charge which is the theoretical equivalent of the actual latency relaxation. The theoretical LR, however, differs in several respects from the actual. The theoretical curve begins at the zero of time, while the actual latency relaxation does not begin, in general, until about 1.5 ms. after the instant of stimulation. This merely corresponds to the fact that, in the muscle,

some reaction concerned with the excitatory process must run its course before resting myosin begins to be transformed into relaxing myosin. This process may be, in part, the release of Ca that Bailey (1942) postulates acts *in vivo* to activate myosin-ATP-ase. There are other deviations of the theoretical curve from the experimental, but these are of secondary importance, and, at any rate, are too detailed to take up here.

The fact that the theory of muscular contraction, outlined above, leads to an overall tension curve that begins with an initial decrease, followed by an increase of tension that agrees in certain respects quite closely with the actual behavior of a muscle tetanus, is presumptive evidence in support of the assumed underlying mechanism. Further corroboration for this view may be found in several other considerations, such as, for example, the possibility that the variation of m_R with time as expressed in Equation (2) provides a definite basis for Brown's (1941) alpha-process. But such discussion must be postponed for the full-length publication of our theory.

It must be stressed that the present discussion deals with the results merely of a preliminary analysis of the basic conceptions symbolized in the schemes of Reactions (I) and (II). As more work is done on this theory, modification in detail will undoubtedly have to be made. Furthermore, the theory deals only with the events of the latent and contraction periods of muscular response. Post-contractile relaxation is not considered. In this connection, it is significant that the theory is deliberately limited in the sense that it does not include some process that restores contracted myosin to its original rested state during this relaxation phase. However, it may be possible to extend the theory so as to make it conform with the view, for which some evidence exists, that special chemical reactions during post-contractile relaxation actively serve to transform contracted into resting myosin.

Finally, it is evident that the theory we have outlined is a particular formulation of the mechanism of activation coupling, and, therefore, in so far as it has merit, it upholds this conception of the energization of muscular activity. Quite apart from this theory and its connotations, however, the general conclusions and inferences of our experiments on the effects of pH and temperature on the latent period of contraction provide independent support for activation coupling comparable to that of Ritchie (1933), Brown (1936), and Buchthal (1944 a and b), previously discussed. Thus, it is clear, in view of the particular

activation mechanism our theory provides, and especially because of the experimental evidence of our own and other research dealing with live muscle, that there is good reason for concluding that activation coupling is the means by which muscular contraction is energized.

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SECTION OF PSYCHOLOGY

MARCH 19, 1945

DOCTOR EDNA HEIDBREDER, Professor of Psychology, Wellesley College, Wellesley, Mass.: *The Attainment of Concepts—A Psychological Interpretation.*

(An abstract of this paper will be published in the May issue of the TRANSACTIONS.)

SECTION OF ANTHROPOLOGY

MARCH 26, 1945

DOCTOR A. KARDINER, New York, N. Y.: *Psychological Criteria for an Intercultural Comparison of Personality.*

(No abstract of this paper has been received.)

SECTION OF PSYCHOLOGY

MARCH 30 AND 31, 1945

Conference on "*Non-Projective Personality Tests.*"

The Section of Psychology held a Conference on "Non-Projective Personality Tests," as the fifth in the series for the Academic Year 1944–1945.

The program consisted of the following papers:

PERSONALITY INVENTORIES

Chairman, Anne Anastasi, Queens College, Flushing, New York.

"Recent Research with the Multiphasic Personality Inventory," by G. Hamilton Crook, Personnel Research Section, Classification and Replacement Branch, The Adjutant General's Office, New York, N. Y.

"The Effect of Alcohol on the Personality Profile (Minnesota)," by Major Harold A. Abramson, (M.C.) A.U.S.

"Psychological Screening Procedures in the War Shipping Administration," by Sanitarian (R), George G. Killinger, Chief, Psychological Service, U.S.P.H.S., and Past Assistant Sanitarian (R), Joseph Zubin, Chief, Medical Statistician, Psychobiological Program, U.S.P.H.S., War Shipping Administration.

THE CORNELL INDEX AND THE CORNELL MULTIPLE CHOICE WORD ASSOCIATION TESTS

Chairman, Henry E. Garrett, Columbia University, New York, N. Y.

"Construction and Standardization," by Bela Mittelmann and Keeve Brodman, Cornell University Medical College, New York, N. Y.

"Results," by Arthur Weider, Cornell University Medical College, New York, N. Y., and David Wechsler, Psychiatric Division, Bellevue Hospital, New York, N. Y.

"Application," by Harold G. Wolff, Cornell University Medical College and New York Hospital, New York, N. Y.

"The Cornell Selectee Index as an Aid in Psychiatric Diagnosis," by Lt. Comdr. Harold J. Harris, (MC.) U.S.N.R.

Ability Patterns and Personality

Chairman, David Shakow, Worcester State Hospital, Worcester, Massachusetts.

"The Expression of Personality and Maladjustment in Intelligence Test Results," by Roy Shafer, Research Psychologist, Menninger Clinic, Topeka, Kansas.

"Personality Diagnostic Evaluation by Means of Non-projective Techniques," by Edith Wladkowsky, Psychiatric Division, Bellevue Hospital, New York, N. Y.

"Difference between Cases with Inventories Giving Satisfactory and Unsatisfactory Results," by Zygmunt A. Piotrowski, Psychiatric Institute, New York, N. Y.

Theory

Chairman, Gardner Murphy, College of the City of New York, New York, N. Y.

"Hypotheses Underlying Non-Projective Tests of Personality," by David Rapaport, Head of Department of Psychology, Menninger Clinic, Topeka, Kansas.

Problems of Performance Analysis in the Study of Personality," by Martin Scheerer, College of the City of New York, New York, N. Y.

ANNOUNCEMENT OF PUBLICATIONS FOR 1945[1]

The following publications will be issued by the Academy during the current year. Members of the Academy who desire to receive these papers will kindly request the Executive Secretary to send them, and they will be mailed, free of charge as they are ready for distribution, except as qualified in the footnotes:[2]

ANNALS

1. "Diffusion of Electrolytes and Macromolecules in Solution." Papers delivered at the conference by this title. (Approximately 146 pages.)

2. "Animal Colony Maintenance." Papers delivered at the conference by this title. (Approximately 130 pages.)

3. "The Effect of Activity on the Latent Period of Muscular Contraction," by Alexander Sandow. Awarded an A. Cressy Morrison Prize, 1945. (Approximately 30 pages.)

4. "A Hitherto Undemonstrated Zoogleal Form of *Mycobacterium tuberculosis*," by Eleanor Alexander-Jackson. Awarded an A. Cressy Morrison Prize, 1945. (Approximately 20 pages.)

5. "Respiration and Germination Studies of Seeds in Moist Storage," by Lela V. Barton. Awarded Honorable Mention, A. Cressy Morrison Prize Competition, 1945. (Approximately 20 pages.)

6. "Surface Active Agents." Papers delivered at the conference by this title. (Approximately 157 pages.)

SPECIAL PUBLICATIONS

VOLUME III

"Experimental Hypertension." Papers delivered at the conference by this title. (To be issued as a cloth bound volume, which will be available at a special rate for Members of the Academy.)

TRANSACTIONS

Series II, Volume 7, Nos. 1–8. These papers are sent to all Members of the Academy, regularly, during the Academic Year. (Approximately 200 pages.)

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[1] Notice of additional publications to be added to this list will be sent to Members later.

[2] Active, Sustaining, Life, and Honorary Members may receive, upon request, a copy of all current numbers of the Annals.

Associate and Student Members are entitled to receive one complete monograph, or up to 150 pages of smaller papers.

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ELECTED MARCH 22, 1945

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